

THE ORIGINS AND AERODYNAMICS OF FLIGHT IN EXTINCT VERTEBRATES

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ABSTRACT. Active (flapping, powered) flight has evolved in only three groups of vertebrates: pterosaurs (late Triassic), birds (late Jurassic), and bats (early Tertiary). Gliding has arisen many times in vertebrates, is a separate adaptation from flying, and does not appear to be a prerequisite for active flight. Skeletal features that distinguish flyers from gliders include modifications of the pectoral and forelimb apparatus, elongation of the distal part of the wing skeleton for thrust, and certain physiological modifications that often leave clues in the skeleton. Soaring evolved in birds and pterosaurs secondarily, after powered flight was well established in both groups: it is a necessary result of phyletic size increase outstripping the ability to meet power requirements for sustained flapping.

The origin of flight can be approached through a combination of phylogenetic, functional, and aerodynamic evidence. A basic question is whether flight evolved in the trees or on the ground. Of the three groups of active flyers, two (pterosaurs and birds) show no trace of gliding antecedents and appear to have evolved flight directly from the ground. Bats show many morphological and phylogenetic indications of an arboreal, gliding ancestry and are very different in all such respects from pterosaurs and birds. The theory of an arboreal origin of flight in birds so far lacks support from phylogenetic and functional-morphologic evidence; arguments in favour of this theory have invoked hypothetical selective advantages of features that either cannot be tested or apply equally to a terrestrial origin. Most of these features were already present in the coelurosaurian dinosaur ancestors of birds. Pterosaurs were structurally and functionally convergent on birds in many locomotory respects, and show *prima-facie* evidence of a cursorial, non-gliding origin of flight.

Aerodynamic considerations of extinct vertebrates have mainly focused on two animals: *Archaeopteryx* (the first known bird) and *Pteranodon* (a specialized Cretaceous pterosaur). Functional inferences from skeletal evidence imply that *Archaeopteryx* was capable of flapping flight, though most 'modern' avian flight features were not developed; it does not seem well built for gliding. *Pteranodon* (a soarer, not a glider), like many large birds, was capable of active flight but probably only used it to take off, gain altitude, and avert danger. All pterosaurs were strong, active fliers and only large size constrained this ability. Aerodynamics of *Pteranodon* have commanded much productive interest, but nearly all models have been based either on (1) a morphologic analogy to bats, which is structurally incorrect, or (2) an aerodynamic analogy to certain low-speed aircraft or hang-gliders, which is both structurally and aerodynamically incorrect. Reappraisal of the anatomy and aerodynamic parameters indicate that *Pteranodon's* flight range was higher and that it was more active and manoeuvrable than previous studies have suggested, and so more comparable to modern soaring birds. Studies of flight in extinct organisms cannot rely solely on engineering models or presumed selective advantages or pressures; they must take into consideration all aspects of phylogeny, function, and aerodynamics.

POWERED flight is a difficult and complex adaptation which commands attention as a truly 'major feature' of adaptive evolution. Aerodynamic requirements are severe, and they constrain the kinematics of the flight stroke (the defining feature of powered flight) and the morphology of the wing into adaptive channels that have converged in several vertebrate lineages. For this reason the problem of the origin of flight is especially approachable in macroevolutionary terms (Padian 1982). By comparing the morphology, phylogeny, and ecology of various kinds of flying vertebrates the evolutionary origins of flight may be studied. This approach shows that, although many features of vertebrate flight are common to all flyers, the differences in morphology and

ecology suggest different evolutionary pathways to the same ends (Pennycuick 1972; Rayner 1981; Padian 1983b).

The purpose of this work is to assess the flying abilities of extinct animals. The first step is to review briefly the several modes of air travel, and to show how skeletal indicators of these modes may appear in the fossil record. A basic introduction to the known fossil flyers is followed by a consideration of the origins of flight in birds, pterosaurs, and bats. Finally, treatments of the aerodynamics of extinct vertebrates are reviewed, and new interpretations suggested.

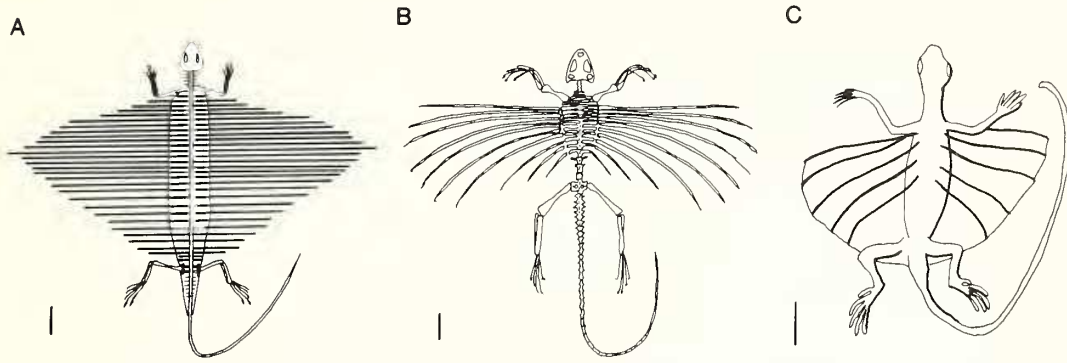
It should be noted that in the present context 'flight' denotes active, powered, flapping flight only. Other modes of air travel that are not self-powered (gliding, parachuting, and soaring) are thereby differentiated; unfortunately space does not permit extensive treatment of the latter. The scope of this review is by no means exhaustive, but is an introduction to current issues. Important problems such as energetics, neurology, and migration must be largely omitted, as there is little direct evidence of them from the fossil record.

TYPES OF VERTEBRATE FLIGHT

Air travel in living vertebrates has often been divided into four modes: parachuting, gliding, flapping, and soaring (Lull 1906; Savile 1962; Hildebrand 1982). These have recently been defined and contrasted by Rayner (1981) in an excellent review of flight adaptations in living vertebrates. Parachuting is usually distinguished from gliding in two ways: the force responsible for the majority of aeronautic support (lift for gliding, drag for parachuting), and the angle of descent (shallower than 45° for gliding, steeper than 45° for parachuting). This can be reduced to a consideration of lift/drag ratio. In evolutionary terms, parachuting may require less morphologic modification, for it is merely a way of slowing a fall; gliding implies a greater horizontal component and a longer time in the air, often with a relatively precise pre-selected landing point. Some authors believe that only radially symmetrical organisms can really qualify as parachuters, though others define parachuting as drag force exceeding lift force. Flapping flight, as its name implies, is defined by the flight stroke, which imparts power in the form of forward thrust. When the resulting increase in air speed from the flight stroke is applied over the surfaces of an aerodynamically efficient airfoil, a pressure differential creates thrust, enabling the animal to gain altitude regardless of assistance from winds or a high starting point. Soaring is a secondary adaptation in large birds and (apparently) large pterosaurs that evolved from flappers and still retain some capacity to flap. Soaring, which has often been likened to falling down an up escalator, allows the animal to make use of thermals (convection rings of rising air) to gain energy that offsets the animal's weight. Such energy may also be gained from winds, as well as from wind speeds that vary with altitude (Pennycuick 1972; Brower 1983). Soaring is both energetically inexpensive and advantageous to predators with acute long-distance vision; the low energetic cost appears to have enabled many soaring birds and pterosaurs to grow phyletically to a size at which flapping for extended periods is energetically impossible. One would think that there is no reason why gliding animals, incapable of powered flight, could not directly evolve a soaring habit. However, gliders have a wing of poor aspect ratio for optimal soaring performance, they cannot easily avoid various kinds of aeronautical hazards, and there are few ecological advantages of soaring to them because they are not visually oriented predators. Rayner (1981) has pointed out that bats do not soar because there are no convective air currents at night. In the absence of selective pressure to become diurnal, seek large prey, and develop acute vision, soaring probably would not be useful for bats. Gliding animals, by virtue of their ecology and diets, also have no reason to soar and it is not surprising that this mode of air travel is largely restricted to a secondary adaptation in groups of predatory and scavenging flappers.

Skeletal correlates of aerial adaptations can provide insight into the aerodynamic abilities of extinct vertebrates. Gliding adaptations are difficult to recognize in the fossil record because they often leave no skeletal clues, and airfoils are seldom preserved. In the absence of an airfoil, adaptations to some form of air travel may be recognized by analogy to modern forms (text-fig. 1). For example, the hyperelongated ribs of the lizard-like *Kuehneosaurus* (upper Triassic, Bristol

Channel: Robinson 1962) and the closely related *Icarosaurus* (upper Triassic, New Jersey: Colbert 1966, 1970) are quite similar to those of the modern agamid lizard *Draco*, which uses its ribs to support a gliding membrane (Colbert 1967). Morphologic features can also indicate functional, aerodynamic, and even physiological abilities and limitations in fossil forms. Several such criteria are available to distinguish active flyers from passive gliders (Padian 1983b).



TEXT-FIG. 1. Three reptiles that modified their ribs as gliding organs. A, *Weigeltosaurus*, upper Permian (after Evans); B, *Icarosaurus*, upper Triassic; C, the living agamid lizard *Draco*. Scale bars represent 2 cm.

1. The defining feature of a flying vertebrate is its flight stroke. Adaptations related to the generation of the power stroke include an expanded bony sternum or breastbone (including a pronounced median keel) for anchoring the flight muscles, a shoulder girdle that is braced to the sternum, an enlarged deltopectoral crest on the humerus for the insertion of flight muscles, and a shoulder articulation that limits forearm movement to activities compatible with the flight stroke (text-fig. 2). Flying vertebrates have developed these features to a relatively greater or lesser degree (bats rather less than birds and pterosaurs in some respects), but such features are never found in the skeletons of gliders.

2. The forelimb proportions in aerial vertebrates are often greater than in non-aerial relatives. Flying squirrels, for instance, have humerus and forearm segments significantly elongated over those of other squirrels (Bryant 1945; Thorington and Heaney 1981). True flyers take this a step further in that the outermost segment of the wing, comprising the wrist (birds), hand (bats), or one finger (pterosaurs), is hypertrophied, which never happens in gliders (text-fig. 2). This is the area that provides thrust (forward motion) in active flight, whereas the inner two wing segments provide lift (on which a glide depends for aerial support: see Rayner 1981).

3. The airfoil in gliders is normally a simple extension of skin and superficial muscle, stretched by bony elements (limbs and bone spars in most gliders, but ribs in others), and without any (or with only rudimentary) internal support structures (Jepsen 1970; Thorington and Heaney 1981; Novacek 1982). In flyers the airfoil is always stiffened by anteroposteriorly oriented structural elements. These are the feather shafts of birds, the fingers of bats, and the intercalated wing fibres of pterosaurs (Zittel 1882; Wellnhofer 1975; Padian 1983b). These may reduce spanwise tension in the wing membrane, a problem noted by Bramwell and Whitfield (1974) for pterosaurs, and equally applicable to bats. Such structural elements certainly act in all flyers to give camber to the wing and to provide competence of the airfoil during the flight stroke.

4. Gliders, which are all arboreal, retain most locomotory abilities of their non-gliding relatives. This is not true for flyers, whose limb structures have been modified to accommodate the kinematics of the flight stroke by reducing unrelated mobility at certain joints, lightening and strengthening

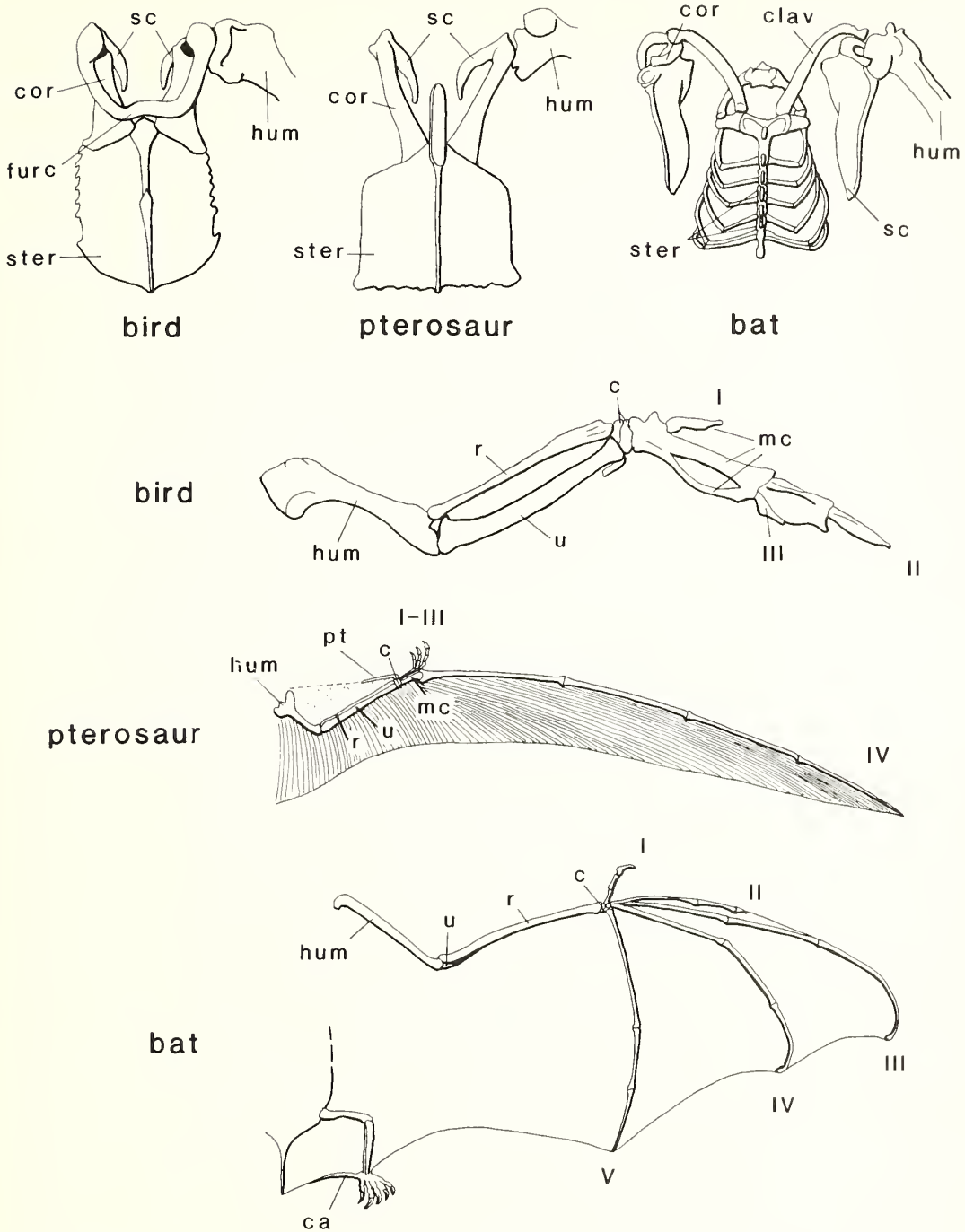
bones, and eliminating unnecessary muscle weight from the wings. Limitations of normal mammalian locomotion are obvious in the bats (except *Desmodus*, the vampire bat, which is secondarily modified for walking and jumping: Altenbach 1979). Ostrom (1976b) demonstrated the restrictions of certain wrist and hand movements in post-*Archaeopteryx* birds, compared to their coelurosaurian dinosaur ancestors. And the limitations on the motion of pterosaur forelimbs, documented by Hankin and Watson (1914), Bramwell and Whitfield (1974), Wellnhofer (1978), and others, have been shown to be modifications related to the down-and-forward flight stroke common to birds and bats (Padian 1983a, b). This stroke and its aerodynamic effects are well understood in living forms (Pennycuik 1972; Rayner 1979).

5. Pneumatic foramina (holes in the skeleton for expansion of respiratory surface into the bone cavities, used to cool the blood), and thermoinsulatory coverings such as feathers and fur, indicate a level of metabolism necessary to sustain active flight. Bats lack pneumatic foramina, though birds and pterosaurs have them. Therefore, whereas such foramina are not necessary for flight, their presence leads to only one inference (Seeley 1870). Pterosaurs and birds, unlike other known diapsids (crocodiles, squamates, and *Sphenodon*), evolved a thermoinsulatory covering. Bats, of course, are furred, but so are other mammals, so this feature by itself does not relate to flight. Indeed, it is not even clear that these features evolved strictly in the context of flight in the other two groups, but knowledge of such fossilized structures is poor.

TRUE VERTEBRATE FLYERS

Pterosaurs have their earliest records in the Norian (upper Triassic) of Italy (Wild 1978), birds in the upper Jurassic of Germany (with apparent occurrences in France and Utah [Jensen 1981]), and bats in the Eocene of North America (Jepsen 1970) and Germany. Pterosaurs died out at the close of the Cretaceous Period, along with all the dinosaurs except birds, which by their coelurosaurian ancestry are properly considered theropod dinosaurs (see below). Pterosaurs coexisted with birds, and have a more extensive and diverse fossil record than birds, throughout the Cretaceous. During this time the record of birds is virtually restricted to open-water forms such as the ternlike *Ichthyornis*, the diving, flightless *Hesperornis*, and its relative *Baptornis* (Marsh 1880). At the close of the Cretaceous some other forms appear, but these are only poorly known (Brodkorb 1963) and only tenuously linked to living orders. Cretaceous pterosaurs are also almost entirely found in marine facies, and have commonly been presumed pelican- or gull-like in their habits. Because the known Cretaceous representatives of these groups evidently had similar ecologies, on face value it may be inferred that pterosaurs did not die out from competition with the birds, but rather from a failure to keep diversifying and replacing taxa, a necessary component of evolutionary persistence. Bats seem to have occupied a nocturnal, originally insectivorous adaptive zone since sometime in the early Tertiary, after the pterosaurs were gone and the birds already well established.

Pterosaurs. Pterosaurs have recently been reviewed and revised by Wellnhofer (1970, 1974–1975, 1978: anatomy and diversity) and Padian (1979, 1980, 1983a, b: locomotion and flight). In light of recent work a summary of salient features of pterosaurs may be given. They were active flyers with a shoulder girdle strongly buttressed to the sternum, which was widely expanded over the ventral thorax and keeled in the midline (Wellnhofer 1978). The sternum anchored the flight muscles, and as in birds the recovery stroke of flight, powered by the *M. supracoracoideus* equivalent, was effected by a pulley mechanism involving the acrocoracoid process of the coracoid, which changed the primitive action of the muscle from an adductor to an elevator (Padian 1983b). The wing could be folded, but the joint separating the second and third of the three major functional units of the wing was between the fourth metacarpal and its phalanx, not at the wrist as in birds (text-fig. 2). The wing was a membrane of skin with a network of closely intercalated 'fibres' that provided strength and camber; these 'fibres' are never found folded but are always gathered, so their structural integrity is evident (Zittel 1882; Wellnhofer 1975; Padian 1983b). They may have been modified scales, and were presumably keratinous. The wing was brought forward through a down-and-forward path



TEXT-FIG. 2. Diagrammatic comparisons of the thoracic regions and forelimbs of the three groups of vertebrate flyers. Thoracic regions (*above*) are seen from the front; right forelimbs (*below*) in dorsal view. Structurally, the coracoids of pterosaurs and birds and the clavicles of bats appear to be analogous, as do the bird's furcula, the cristospine of pterosaurs, and the manubrium of bats; the last two structures are situated at the anterior extreme of the sternum. Abbreviations: *c*, carpus; *ca*, calcar; *clav*, clavicle; *cor*, coracoid; *furc*, furcula; *hum*, humerus; *mc*, metacarpus; *pt*, pteroid; *r*, radius; *sc*, scapula; *ster*, sternum; *u*, ulna; I-V, numbered digits. Not to scale.

during the flight stroke, and retracted by an up-and-backward motion, as in birds and bats (Padian 1983*b*). The hindlimbs were sufficient for bipedality to be the only means of terrestrial locomotion; pterosaurs could not walk on all fours because the forelimbs could not rotate past the limit of the forward flight stroke (Padian and Olsen 1984; Padian 1983*b*). The femur was held in a diagonal to horizontal position nearly parallel to the body midline, as in birds and most dinosaurs, and the gait was parasagittal and digitigrade (Padian 1983*a, b*). The Pterosauria comprise some forty genera, traditionally divided between the paraphyletic Rhamphorhynchoidea and their monophyletic descendants, the Pterodactyloidea; diagnostic differences are reviewed in Wellnhofer (1978) and Padian (1980). Pterosaurs, though not dinosaurs, were very closely related to them and share with them many synapomorphies (Gauthier 1984); their closest known sister taxon appears to be the small ornithosuchian archosaur *Scleromochlus* (von Huene 1914; Padian 1980, 1984; Gauthier 1984).

Birds. The fossil record of birds begins with *Archaeopteryx*, from the upper Jurassic Solnhofen limestones of Bavaria. The history of the five known specimens (plus the original feather) has often been reviewed (see e.g. Ostrom 1979 and references therein). Even more frequently repeated is the concept of the mosaic 'half-reptile, half-bird' morphology of *Archaeopteryx*, although until recent years there was no convincing picture of which 'reptiles' included the direct ancestors of birds. Ostrom, in a series of papers (1973–1979), established that birds were descended from small coelurosaurian theropod dinosaurs, on the basis of a series of unusual and generally overlooked characters that were unique to these dinosaurs and birds (represented by *Archaeopteryx*). Padian (1982) formalized Ostrom's evidence and arguments, along with additional evidence, into a testable cladistic framework in which some fifty synapomorphies of *Archaeopteryx* and coelurosaurs were recognized; Gauthier (1984) has expanded this list to over 120 (Gauthier and Padian, in press). Critics of Ostrom's theory (e.g. Walker 1977; Tarsitano and Hecht 1980; Martin *et al.* 1980; Martin 1983) have quarrelled with interpretations of individual characters or have argued that some proposed synapomorphic features are 'not similar', and have pointed out resemblances of either *Archaeopteryx* or modern birds to other selected fossil archosaurs. However, these critics have not recognized or addressed the structure of cladistic methodology, which is a valuable tool for reconstructing phylogeny precisely because it transforms mere lists of characters (e.g. Martin 1983) into hierarchical distributions of nested sets of characters, thereby forming a more robust logical structure than a list. In this context, non-hierarchical claims of 'similarity' or 'dissimilarity' have no objective meaning. Statements about sister-group relationships between two taxa must be gauged against a third in order to establish phylogenetic homology; the latter is deductive, not declarative, and so, logically, are statements about 'dissimilarity' (non-homology at a given phylogenetic level).

As Martin (1983) and others have pointed out the coelurosaurian hypothesis is based almost exclusively on an extensive series of post-cranial characters (though the skull of *Archaeopteryx* is in all recognizable respects coelurosaurian), which ostensibly evolved independent of the others. Ostrom compared these across a wide range of coelurosaurs and other archosaurs. Walker (1973) and Martin *et al.* (1980), who advocate a common origin of crocodiles and birds (among as yet unspecified 'thecodonts'), have mainly relied upon certain features of the ear region which are unfortunately not preserved in the crucial coelurosaurs. Because two-thirds of a comparison cannot establish anything with respect to the other third, at present the evidence of the ear region is only tantalizing, though potentially quite valuable. Critics of Ostrom's post-cranial theory though have yet to demonstrate or even propose that any other specified taxon is closer in these respects to *Archaeopteryx*; consequently, it must be provisionally accepted that birds are descended from theropod dinosaurs—in fact, they are the closest sister-group of deinonychosaurian coelurosaurs (*sensu* Colbert and Russell 1969; see Padian 1982, and Gauthier and Padian, in press).

This phylogenetic premise is necessary to understand which skeletal features conventionally regarded as 'avian' are really avian and not simply dinosaurian, theropodan, or coelurosaurian. The typical textbook litanies of 'avian' characters include hollow bones, a lightly built skeleton, long forelimbs, fused clavicles, and a keeled sternum; yet all these features are already synapomorphies of coelurosaurian dinosaurs, and the last is not preserved in *Archaeopteryx* (Gauthier and Padian, in

press). At present the only known character distinguishing *Archaeopteryx* as a bird is the flight feathers, which demonstrates that *Archaeopteryx* was an active flier (Feduccia and Tordoff 1979). Later birds are distinguished from *Archaeopteryx* by the fused and reduced wrist and fingers, and the ossified contact of the coracoid with the expanded sternum, both modifications for flight; and by the fusion of pelvic elements, reduction of teeth, and various cranial features. These, however, must be regarded as ancillary to the origin of birds; in an adaptive sense they can be viewed as fine-tuning the flight mechanism and the avian life-style.

Bats. Evidence for the origin of bats is indirect. The earliest fossil bat is *Icaronycteris*, from the Green River (Bridgerian: middle Eocene) of Wyoming (Jepsen 1970). Its complete skeleton, magnificently preserved, has been subjected to some phylogenetic debate, but most workers prefer to assign it, with some reservations, to the Microchiroptera. It has a long tail and many other primitive features, but it is in all respects a flying bat, with fully developed wings. Possible dental records of bats from the early Eocene are provocative but shed no light on the question of bat origins; spectacular skeletal fossils from the Middle Eocene (Lutetian) Messel pits of the Darmstadt region of Germany represent several species of primitive bats. Recent re-evaluation of several ancient, generalized, closely related placental groups (including the Scandentia or tree shrews, bats, primates, and lipotyphlan insectivores) suggest that dermopterans and bats are sister groups (Novacek 1982). If this view prevails the understanding of plesiomorphic characters and ecological factors in the origin of bat flight may fit a cohesive evolutionary pattern (see below).

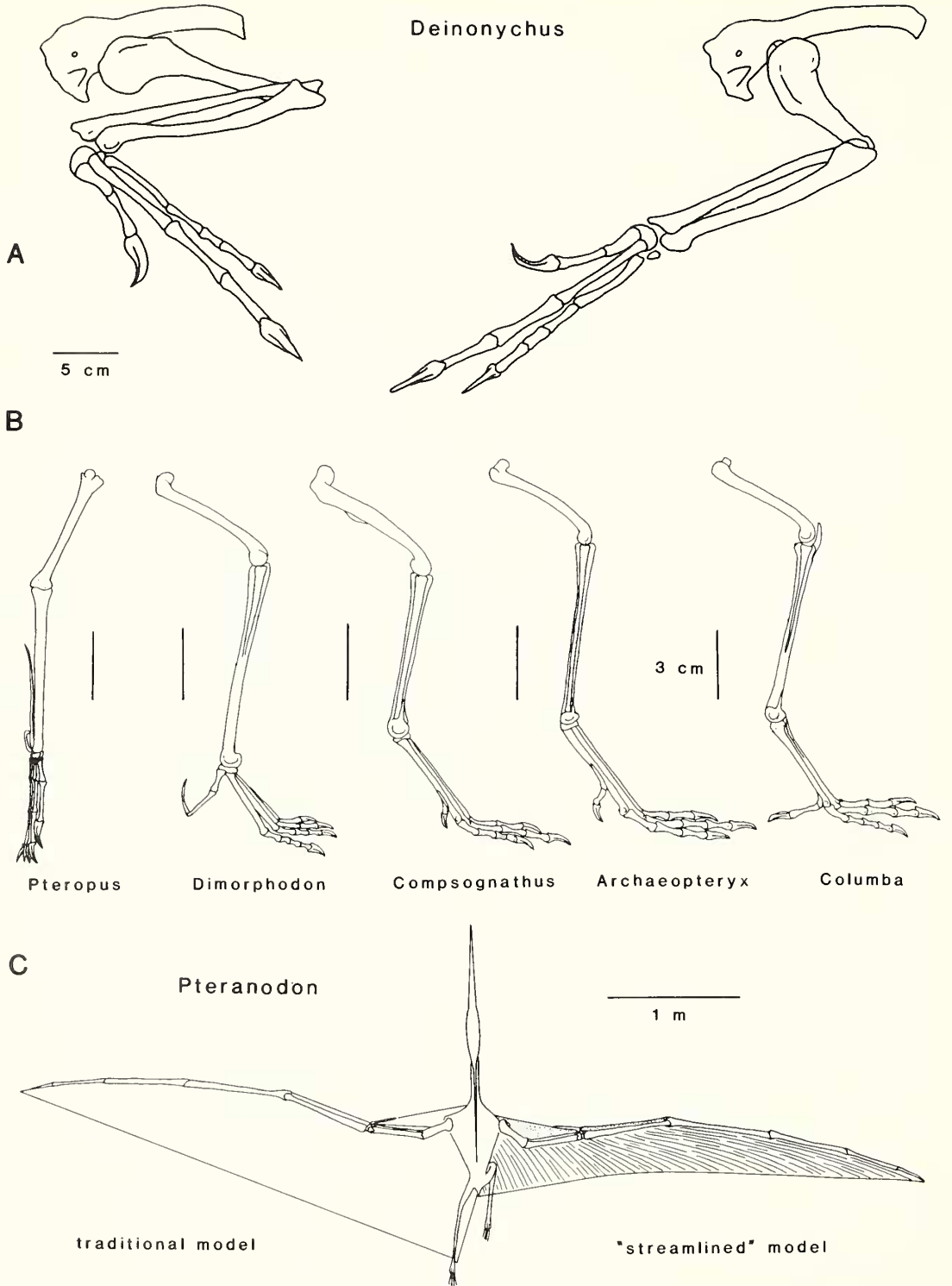
ORIGINS OF FLIGHT

'Origins' has been left plural because mounting evidence suggests that pathways to vertebrate flight have differed, depending as much on phylogenetic constraints as on aerodynamic ones. Powered flight is defined here by the common use in all flyers of the down-and-forward flight stroke of the wings. The wing produces both lift (inner segment) and thrust (outer segment). How such wings evolve is not so clear-cut. In order to be convincing, explanations of the evolution of flight must be consistent with empirical knowledge. Evolutionary theory can support many kinds of adaptive explanations, but only a fusion of many independent lines of evidence can suggest which historical explanations are more appropriate in a given case (Padian 1982).

Bird flight. Far more attention has been paid to birds than to bats and pterosaurs with regard to the origin of flight. Ostrom (1974, 1979) reviewed the old dichotomy between the terrestrial, cursorial origin ('from the ground up': Williston 1879; Nopcsa 1907, 1923)—obscure and unsupported by evidence for nearly a century—and the arboreal, gliding origin (Marsh 1880; Bock 1965), which has predominated in evolutionary thought. The latter is intuitively more convincing, perhaps because the images of climbing, leaping, parachuting, gliding, and finally flapping sail past our eyes like cartoons in a flipbook. The question is not whether this theory is possible; I will argue later that it is, at least for bats. The question is really whether it is supported by evidence; and so far the answer is surprisingly negative, at least for birds. This is odd considering the reliance most modern birds place on arboreal life; however, to study the origin of flight is not to deal with why modern birds live in trees, but how ancient birds got into the air. *Post hoc* arguments are not applicable.

Bock (1965) championed the arboreal theory by showing that it was consistent with the neo-Darwinian Modern Synthesis of evolution—invoking no teleology and no inadaptable stages, with each adaptive level self-sufficient and derivable from the previous one by small steps. Selective advantages of each intergrading stage were self-evident, on the basis of their survival and success in modern forms. But as valid as these assumptions may be, they hold true regardless of any empirical evidence that may be brought to bear on the origin of birds and their flight. Bock's theory, in the absence of evidence, reduces to a statement of belief that flight evolved in accordance with the Modern Synthesis; but many possible explanations can be accommodated by the Synthesis. The point at issue is to discover which factors could discriminate between alternate theories.

There are at least three kinds of factors at work: phylogenetic, functional, and aerodynamic



(Padian 1982). Phylogenetically the most robust hypothesis is that birds began from small, active, carnivorous, bipedal theropod dinosaurs. As Ostrom (1974) realized, any satisfactory theory of bird origins has to begin with *Archaeopteryx*; and any satisfactory theory of *Archaeopteryx* must consider the habits of its closest sister-group. This, the predatory Deinonychosauria, included agile, terrestrial, cursorial bipeds with long arms, large brains, and stereoscopic vision (Hopson 1980; Russell 1980; Ostrom 1980). Trends toward these features in the evolution of coelurosaurs is clear (Padian 1982; Gauthier 1984; Gauthier and Padian, in press). Though perhaps nothing about the skeletons of these animals, including *Archaeopteryx*, precludes at least the smaller forms from climbing trees, no evidence favours it (Ostrom 1979)—despite a wealth of skeletal correlates in modern birds for scansorial and arboreal adaptations (Feduccia 1973; Bock and Miller 1959). Therefore, unless compelling arguments can be adduced for an arboreal stage in the evolution of flight, it seems to me that the phylogenetic and palaeoecological evidence of terrestrial ancestry must be taken at face value.

Coelurosaurs had many structural features that later figured in the evolution of flight. These attributes may be adduced from the extensive skeletal comparisons of coelurosaurs and other archosaurs by Ostrom (1974–1976). Some of these have a direct relationship to the later development of the flight stroke in birds. In addition to the anatomical features mentioned above, Ostrom (1969) noted the semilunate wrist joint in deinonychosaur (text-fig. 3A), which allowed them to flex their long hands laterally against the forearm—in fact, to fold them exactly as a bird folds its wing (Ostrom 1976b). *Archaeopteryx* shows no specialization of the forelimb bones beyond those of other deinonychosaur, and the bones themselves are only slightly longer proportionally than in its larger, non-volant relatives. Direct palaeontologic evidence indicates that deinonychosaur used the forelimbs to grasp prey while attacking it with the teeth and clawed feet (Kielan-Jaworowska 1975)—just as Ostrom (1969) had predicted. To seize prey from a retracted position the humerus must be protracted and adducted, the forearm extended, and the hand extended by swinging forward and mediad, pushed in part by differential movement of the radius relative to the ulna (text-fig. 3A). (When the elbow is flexed the radius slides forward over the ulna and flexes the long hand against the forearm, as in birds.) The shoulder joint is a ball and socket with only partial restriction of movement, the elbow is a hinge, and the wrist another hinge; the mobility of these joints is equivalent to or greater than those of birds, and restricted in similar ways. Therefore only the smallest conceivable modification is necessary to change the functional repertoire of the deinonychosaurian forelimb to accommodate the down-and-forward motion of flight. Because these structures and functions were useful in a very different context for terrestrial predators, it cannot be argued that they evolved specifically for flight. They were co-opted from a predatory function, and this would only have been possible in a terrestrial setting, as Ostrom (1974) explained:

Climbing and flying involve different sets of muscles and require very different movements of the various forelimb components. In all probability, selective forces that tended to perfect one activity would not have been optimal for the other. And while we can rationalize the advantages of climbing into trees as a necessary precursor to the earliest stages of the evolution of flight, from a functional anatomical aspect the two activities are unrelated.

TEXT-FIG. 3. A, left pectoral girdle and forelimb of the coelurosaurian dinosaur *Deinonychus*, in lateral view: left, with arm folded, right, with arm extended. The semilunate carpal synapomorphic of deinonychosaur and birds is at the base of the three digits. B, right hindlimbs in lateral view: the fruit bat *Pteropus*, the pterosaur *Dimorphodon*, the small theropod dinosaur *Compsognathus*, the first known bird *Archaeopteryx*, and the pigeon *Columba*. Note the differences in orientation, femoral head, fibular location, and metatarsal-phalangeal structure between the bat and the four archosaurs; the former hangs upside-down in trees, whereas the latter are and were presumably active terrestrial bipeds. C, dorsal view of the Cretaceous pterosaur *Pteranodon* in flight: left side, the traditional 'wide-winged' model, after Bramwell and Whitfield 1974; right side, the revised 'streamlined' model based on new analysis of the forelimb and hindlimb articulations (Padian 1983b), and on wing impressions preserved in the genus *Rhamphorhynchus*.

What of the role of feathers? Most workers have accepted Regal's (1975) contention that feathers evolved initially as modified scales to enhance thermoregulation, though whether to shed heat, retain it, or both, depends on answers to palaeoenvironmental and palaeophysiological questions that may never be resolved. In any case, Regal's thoughtful analysis applies only to body feathers (down and contour); flight feathers are clearly specially modified contour feathers, and their insulatory function when folded is almost certainly secondary in an evolutionary sense to their development as a flight organ. Ostrom (1975*a, b*) proposed, following the predatory ecology of the coelurosaurs, that hypertrophied feathers on the forelimbs were selected as an aid to batting down flying insects. Although this use is consistent with generally distributed predatory traits in theropods, it is difficult to see how the improvement of a predatory function such as this would have paved the way for the development of flight, a locomotory function (Padian 1982). (Ostrom produced a parallel argument, quoted above, to dispel the arboreal theory's putative connection between climbing and flying.) Martin (1983) commented that a solid mesh of feathers was a poorly designed 'net' that probably would have only blown the insect prey farther away. Caple *et al.* (1983) showed that the 'insect nets' would have generated severe instability and loss of balance. They proposed instead that if the earliest birds and their immediate forerunners caught prey with their teeth instead of their hands, the arms would have been very effective bilateral stabilizers during a jump into the air. Even a forelimb surface expansion capable of lifting 1% of the animal's body weight would have had a significant effect on stability. A greater surface area would result in even greater stability, which, combined with faster takeoff speed, would result in increased lift, a longer time in the air, and presumably a more successful insect forage. Ostrom and most workers have since conceded the advantages of this model (Lewin 1983).

Caple *et al.* (1983) made the terrestrial flight model a strong contender by overcoming the objection that when the winged proto-bird leapt into the air it would immediately lose speed from its only source of power (the legs). The authors set up the basic requirements for the evolution of the flight stroke itself, but did not pursue it to the specific case of birds; I have shown that this stroke is almost fully evolved already in deinonychosaurs, though nearly inconceivable in any other contemporary animals. Any protraction and extension of an airworthy, feathered forelimb would have increased lift and time in the air—whether useful for pursuit of prey (Ostrom 1975*a, b*), escape from predators (Harrison 1976), or simply more agile running over broken ground (Padian 1982), is not important. Any repetition of such a stroke sustains the animal in flight even longer. From these modest beginnings the flight of birds evolved by steps no less adaptive, incremental, or self-sufficient than those of the arboreal scenario. The difference is that ecological stages for which no evidence exists are not invoked. (See Harrison 1976 for several perceptive comments on this issue.)

The fossil record indicates that the immediate ancestors of birds were terrestrial, agile, bipedal, cursorial, and predatory. It does not indicate that they were arboreal, climbers, parachuters, or gliders. Bock (1983) suggested that feathers would have evolved to advantage in treetops, where heat loss is allegedly greater than on the ground; that stereoscopic vision would have been useful for proto-birds clambering through branches; and that long feathers would have helped break an accidental fall from the trees. These hypothetical advantages have yet to be supported by evidence for arboreality. Martin (1983) asserted that *Archaeopteryx* 'was more adapted for moving about in the trees than for a life in the open plain', based on an analogy to primates. His contention that *Archaeopteryx* could not run or even stand fully erect hinges on an interpretation that the proximal femur is obliquely oriented in the acetabulum; however, this orientation applies to dinosaurs, modern birds, pterosaurs, and most mammals, all of which walk parasagittally (text-fig. 3B). This advanced condition is sharply contrasted with the 'semi-erect' condition in 'thecodonts' and crocodiles, all of which have a primitive sigmoid femur with a head that is continuous with the shaft, not set off by a distinct neck. The mobility and anatomy of every joint in the hindlimb of *Archaeopteryx* must be considered; Martin (1983) dealt only with the long proportions of the hindlimb, which he suggested was an adaptation to jumping. He did not detail his scenario in which 'a small arboreal reptile with a tendency toward bipedality . . . [which] was improved by vertical climbing

and leaping', developed flight, nor how fully terrestrial abilities might have re-evolved. It seems, on balance, that many unnecessary steps must be invoked only to get the trees in there somehow. Though both hypotheses demand further work, most workers in the recent literature seem to have accepted Ostrom's ideas on the anatomy, phylogenetic relationships, and functional morphology of *Archaeopteryx* (e.g. Bakker and Galton 1974; Wellnhofer 1974; Desmond 1975; Padian 1983a, b; Thulborn and Hanley 1982; Gauthier 1984; Cracraft 1977; Colbert 1980; Russell 1980; Hotton 1980; Bakker 1980; Halstead and Halstead 1981; McGowan 1980; Caple *et al.* 1983; etc.). The aerodynamic model of Caple *et al.* (1983) promises to be highly productive in further investigations of the evolution of bird flight (Lewin 1983).

Bat flight. The question of the origin of bat flight is in some ways at about the same stage as the question of bird flight was a decade ago, perhaps because so little is known about the ancestry of bats. Once Ostrom proposed a specific origin of birds the question of the origin of their flight assumed a whole new dimension, because models could be constructed on actual taxa. This was particularly important with birds because they have no living relatives that are the least bit like them ecologically.

Though the fossil record does not reveal much about the origin of bats, they share a close common ancestry with other orders of small mammals of nocturnal, arboreal, insectivorous, or omnivorous habits (lipotyphlan insectivores, Dermoptera, and Scandentia). Dermopterans are at least as ancient as bats, if the fossil record gives any indication. However, no one would propose that the modern dermopteran is a plausible *Urtyp* for the earliest bat: for reasons laid out by Jepsen (1970) the colugo is highly specialized for its inverted, fruit-eating lifestyle. But the forests in which the colugo now lives were certainly not always of their present compositions, and therefore it is reasonable to assume that dermopterans have changed with their environment, as bats have. It is highly probable that in the early Eocene or Palaeocene the members of the two groups looked more like each other than their modern representatives do.

Perhaps from these considerations a general idea of proto-bat ecology may be extrapolated. Let us assume, as nearly all workers on the problem have, that the ancestors of bats had the ecological characteristics noted above. As in many primitive mammals, there may also have been a rudimentary sense of echolocation, though perhaps the mechanism was not homologous to the organs used in chiropteran echolocation. Because these features are generally distributed among the sister-groups of bats, no special explanation of the adaptive value of these characters to bats is necessary. At this point, to go further in the investigation of the origin of bat flight requires a more specific statement about the closest sister-taxon of bats. If, for example, the Dermoptera were so established (Novacek 1982) the investigation is reduced to three alternatives: (1) bats did not go through a gliding stage, and evolved powered flight completely independently of the dermopterans' evolution of gliding; (2) the common ancestors of bats and dermopterans went through a gliding stage, and the two lineages subsequently diverged; (3) bats and dermopterans independently evolved a gliding stage, and the bats went on from there to evolve powered flight. The phylogenetic milieu is a powerful source of information about the context of functional evolution. Without a better fossil record of the earliest bats and proto-bats the most promising line of evidence for the origin of bat flight would seem to be analysis of the interrelationships of known orders and the trends that mark their histories. However, some interesting ideas and approaches of previous workers suggest that even in the absence of phylogenetic information, the functional problem can be explored.

Jepsen (1970) proposed three stages in the evolution of bat flight. Stage 1, the pre-bat, was much like the animals described above, except that Jepsen postulated 'large (and, possibly, webbed) front feet' useful in leaping after prey, with hind legs and feet that 'could be extended outward (laterally) from the body when it moved around in crevices'. It also could hang by its hind feet, as flying squirrels can, and could leap from this posture to a nearby target. Stage 2, the sub-bat, had 'webbed large hands (or small wings) which were used principally in catching flying prey', and the proto-wings of skin 'enabled the sub-bat to be very briefly sustained in the air by rapid flapping' after prey. The legs were now fixed laterally. Stage 3 is the essentially modern bat, with fully grown wings and

refined skeletomuscular adaptations. It is important to note that Jepsen did not believe that bats ever passed through a gliding stage: he regarded gliding as a separate evolutionary plateau (or dead end). Instead, like Ostrom, he placed great reliance on the hypertrophy of the hands as prey-catchers.

Two problems with this are: (1) how did a (normally) quadrupedal mammal get around in trees with these large webbed hands, and (2) once again, why should the improvement of a predatory function pave the way for a locomotory function? The evolution of inverted posture is indeed very important, and (as Sam McLeod once suggested to me) may have evolved well before the other features: otherwise, how would the forelimbs be freed for flight? Once suspended upside down, it is easier to drop to a lower target than to climb up, so presumably the advantage of a gliding ability is not eliminated (see below).

Smith (1977), working from the model of a typical gliding proto-bat, regarded the expansion of the wrist and hand membranes almost as a developmental by-product of elongating the digits along with the other forelimb bones. (Fair enough, but why then do not other mammalian gliders have hypertrophied hands?) He suggested that 'the continued development of the wing, in this manner, eventually would have produced an ungainly and clumsy structure that necessitated movement as a wing rather than a fixed gliding device'. The theory stresses the random nature of raw materials upon which selection may act, but the development of the flight stroke and the form-function complexes of bat limbs and girdles is left unexplained. Smith, however, concluded that bats passed through a gliding stage. His view contrasts with that of Pirlot (1977), who suggested that bat flight began as brief periods of hovering while jumping at insects from the ground, again without a gliding stage. Clark (1977) argued against this because the curve of power requirements for increasing flight speed is U-shaped; therefore it would have been far less costly for bats to begin with medium-speed flight, because hovering is as expensive as high-speed flight. Clark concluded that 'it is more reasonable to suggest that bat ancestors were gliders which gradually evolved the capacity for sustained (and controlled) flight at speeds where power requirements were minimal'.

One argument in favour of a gliding origin for bats is that, if their ancestors were indeed arboreal, they would almost have had to have been gliders first: an animal that experiments with powered flight in the treetops risks mortal danger at each outing without some kind of airfoil to break the fall. Evidence for such a glider-type design is found in the configuration of the wing in bats, the only flyers to incorporate the hindlimbs into the airfoil, as all mammalian gliders do (Padian 1982). Without a gliding stage, it must be postulated that the legs became incorporated into the wing only after flapping flight evolved, which did not happen in birds or pterosaurs. An alternative is that enlargement of the hand, and evolution of the flight stroke, occurred in bats after the gliding habit was established. The gliding membrane could have been the 'safety net' for the evolution of flight in an arboreal setting.

Pterosaur flight. The section is quite brief because there is almost no discussion of the origin of pterosaur flight in the literature. This is hardly surprising, as most writers have considered pterosaurs mere gliders, and their exact phyletic origins have not been well understood. Von Huene (1914) suggested that pterosaurs evolved from small arboreal 'thecodonts' like *Scleromochlus*, which jumped from branch to branch, then developed parachuting, gliding, and flapping flight. Romer repeated von Huene's origin of flight theory nearly verbatim in all editions of his *Vertebrate Paleontology*, but leaving out mention of *Scleromochlus*, which he considered a dinosaur. Elsewhere I argue the opposite (Padian 1984): that von Huene got the phylogeny right, but the scenario wrong. *Scleromochlus* is the closest known sister-group to pterosaurs, as von Huene thought (Padian 1980; Gauthier 1984). But in locomotory adaptations it was a small, light, bipedal runner, and so were pterosaurs for nearly the first hundred million years of their existence (upper Triassic-upper Cretaceous).

Pterosaurs parallel birds in so many adaptive respects that every argument applicable to the terrestrial theory given above for birds also applies to pterosaurs (Padian 1983b). They stood, held their limbs, and moved their joints in almost exactly the same ways (text-fig. 3B), and such adaptations as the acrocoracoid process of the shoulder girdle, the restricted glenoid fossa, the

coracoids buttressed to the sternum, the narrow wings unconnected to the feet, the pelvic configuration, the reduced fibula, and the mesotarsal ankle suggest, even with the regrettable paucity of supporting fossils, that pterosaurs evolved flight in a cursorial, terrestrial context, without a gliding stage. They never developed an avian-style perching foot, their hind claws were never sharply curved (unlike their fore claws), and they always kept a low femur/tibia ratio and a high metatarsal/tibia ratio characteristic of lightly built, active animals (Coombs 1978), and uncharacteristic of non-avian arboreal forms. Perhaps they could climb trees; but as in the earliest birds, no evidence currently supports this point, whereas ample evidence indicates high proficiency as terrestrial bipeds. The origin of the first group of vertebrate flyers, unfortunately, is far more poorly known than the origins of flight in the other two groups, and their comparative biology far more difficult to approach.

AERODYNAMIC PERFORMANCE OF FOSSIL VERTEBRATES

Apart from calculations made by Colbert (1966, 1967, 1970), Evans (1982), Thorington and Heaney (1981), and others of the weight, wing area, and wing loadings of various gliders, studies of aerodynamic performance in fossil vertebrates have centred on two animals: *Archaeopteryx* and *Pteranodon*. In both, estimates have been made of gliding performance, with some consideration of minimal power requirements for flapping flight.

Archaeopteryx. It is important to remember that most work on the aerodynamics of *Archaeopteryx* preceded Ostrom's hypotheses of theropod ancestry and terrestrial origin of flight. In this aerodynamic work it was assumed that *Archaeopteryx* was arboreal and mainly a glider, which flew weakly if at all. If Ostrom's ideas (later modified and developed mathematically by Cople *et al.* 1983) are correct, a gliding stage would have been aerodynamically obviated, because gliding from the ground up is so ineffective. There is no way to tell how much, if any, gliding *Archaeopteryx* did, but there is certainly value in estimating its gliding performance, as well as its power requirements.

Flying animals can glide at a range of speeds, merely by varying the incidence of the glide. They also flex the wings at high speeds in order to obtain a range of glide performance (J. M. V. Rayner, pers. comm.). Gliding performance is maximized when the gliding angle (proportional to the sinking speed) is low, because the lift is high relative to drag. But if the lift is too high, the animal slows until it stalls. The minimum flying speed (V_{\min}) is achieved when lift is maximized ($C_{L\max}$: just before stalling) and is inversely correlated with it. This is expressed by the formula

$$V^2 = 2W/\rho SC_L$$

in which W , the weight (mass \times gravity), approximates the lift (L) in a steady glide, ρ is the density of air, and S the area of the airfoil. $C_{L\max}$ is best calculated empirically, and ranges from 1.3 to 1.6 in modern birds and bats (Pennycuik 1972). Because ρ is usually assumed, the critical biologic variables are the weight and wing area, the quotient of which is called the wing loading, and is roughly proportional to gliding speed.

The aerodynamic analysis, then, begins with calculations of weight and wing area. Heptonstall (1970) confirmed Jerison's (1968) estimate of the former at 500 g, and calculated the wing area at 373 cm², exclusive of body and tail surfaces. Bramwell (1971) and Yalden (1971a) argued for lower weights (200–250 g) and larger lift areas (479 cm², including 91 cm² on the body between the wings). Yalden (1971b) compared *Archaeopteryx* to birds of similar wing span (58 cm) and found a weight range of 170–300 g; the same range was found for mammals of similar head–body length (21.8 cm). Yalden used estimates of 150, 200, and 250 g in his calculations, favouring the intermediate value.

Heptonstall (1970) used the formula given above to calculate what he believed to be the maximum flying speed of *Archaeopteryx* at 20.9 m/s. Heptonstall calculated L by estimating maximum bending moments possible on a humerus with a tensile strength commensurate with experimental results, thus deriving the maximum lift possible. In his formula the expression L was equated with W , a common practice when calculating performance in a steady glide, in which maximum lift is generated

(Pennycuik 1972). However, Bramwell (1971) argued that the formula only works for minimum speed (V_{\min}): maximum lift is not generated with maximum speed, and vice versa. Yalden (1971*b*), using a similar formula from Pennycuik (1969), calculated the minimum power speed at 6.9, 7.6, and 8.2 m/s, depending on the weights listed above. Because in modern birds some 15% of body weight is pectoral muscle, Yalden took 30 g as the available weight for the power stroke, and derived a power requirement of 105–140 watts/kg. All these figures are well within avian range, but Yalden noted that this is not surprising, as he based all estimated values on those observed in modern birds. He concluded that if *Archaeopteryx* approached modern birds in muscle physiology, it probably could have flown.

The important point to be made about all the work discussed above is that the calculated values are within the ranges of modern birds. Despite differences in estimates and derivations the results agree to within a factor of two, and usually much closer, and are therefore reliable if not precise. In this context it is interesting to consider Yalden's estimates of minimum power speed, the speed at which the least work has to be done. Once again, the U-shaped curve relating power requirements to flight speed shows that very low and very high speeds are most expensive. Starting flight from a standing position, then, requires a lot of energy to be expended initially, before getting up to an economical speed. A running takeoff can minimize the effort required by the wings to build up this speed, and if the wings are merely spread significant lift can be generated. Caple *et al.* (1983) based calculations on a cursorial model of 100 g, shaped as a cylinder 15 cm long and 3 cm diameter, and applied a ground speed of 3–4 m/s derived from empirical observations by Taylor (1973). Because maximum running speed is observed to vary proportionally with mass, it is clear that an animal the size of *Archaeopteryx*, endowed with the cursorial skeletal adaptations of coelurosaurs, would have had no trouble bringing its ground speed up to minimum flying speed.

Once in the air, the flapping performance can be estimated only if the physiology is known or assumed. The gliding performance depends on wing loading and aspect ratio (the shape of the wing: wingspan squared divided by wing area). Of great importance is the ability of a flying animal to land. To land slowly and easily, most animals reorient the body and beat the wings vigorously to achieve minimum speed flight. (This discussion applies only to landing on the ground, as Caple *et al.* (1983) have shown the difficulty of landing on a branch to an animal that is not already extremely sophisticated in its flight.) Heptonstall (1970) reckoned that the high wing loading and sinking speed of *Archaeopteryx* would have made landing very rough, though Bramwell (1971) figured that the tail would have reduced the stalling speed; Yalden (1971*b*) and Bramwell (1971) both calculated lower wing loadings. In view of the cursorial adaptations of *Archaeopteryx*, it may be surmised that a running landing was possible, so that the airspeed need only have been reduced to the minimum flying speed in order for the legs to take over. Heptonstall (1970) calculated optimal gliding speeds at 10–15 m/s, but the lower wing loading suggested by other authors would have reduced this figure considerably. By my calculations, stalling speed for *Archaeopteryx* would have been on the order of 5–6 m/s, and a short burst of flapping (generating enough lift to slow airspeed) would have enabled a running landing at a speed of 3–4 m/s. (Use of the alula in landing was probably not available to *Archaeopteryx*.)

Pterosaurs. Fascination with the aerodynamics of these extinct archosaurs began well before man invented powered flight. Early work particularly reflected the hope that pterosaurs would reveal possibilities for human flight, though as soon as workable aircraft were invented interest in pterosaurs quickly cooled. In the past decade it has been rekindled by the opposite hope, that modern advances in aviation might reveal how pterosaurs flew.

Most attention by far has centred on the crested pterodactyloid, *Pteranodon*. *Rhamphorhynchus*, an earlier, smaller, long-tailed form, was studied by von Kripp (1943) and a flapping model built and flown by von Holst (1957); however, the model would work properly only when the leaf-shaped vane at the end of the tail, preserved in several fossil specimens, was oriented horizontally, whereas its true orientation is vertical. Apart from these studies, modern work has been almost entirely devoted to *Pteranodon*, and a general overview of this work will now be given.

The problem initially faced was to determine the upper size limit of *Pteranodon*, because until 1975 it was believed to be the largest flying creature of all time. Most studies drew material from the worn and broken bone ends of the *Pteranodon*-like *Ornithocheirus* in the Cambridge University collection, or from the more complete but thoroughly crushed material of *Pteranodon* itself in the Yale University collections (described by Eaton 1910). A typical wing span used in the modern aerodynamic work is about 7 m (Heptonstall 1971; Bramwell 1971; Bramwell and Whitfield 1974; Brower 1983; etc.), though Eaton described a partial radius and ulna that, if projected isometrically, would have yielded a wing span of 8.16 m (Heptonstall 1971). My study of the Yale collections and Eaton's work reveal that the largest size for which complete wings exist is about 5 m. Even at this size, measurements from many incomplete specimens must be pooled in order to arrive at a mean figure. The exact size of the largest *Pteranodon*, however, matters little because in 1975 Lawson described remains of a pterodactyloid he later named *Quetzalcoatlus northropi*, which had a wing-span initially projected at 15.5 m. This estimate proved to be too high, and a figure of about 12 m (35–40 ft), based on additional material and further proportional comparisons, is now generally accepted (Langston 1981). Numerous remains of apparent juveniles of this species, almost exactly half the length of the larger form in all dimensions, have a wing span of approximately 5.8 m (19 ft).

An up-to-date review of aerodynamic assessments of *Pteranodon* and its relative *Nyctosaurus* was given by Brower (1983), which obviates long discussion here; I will summarize only the major outlines and conclusions of other authors (Table 1), and point out possible directions for future research. The most influential work, of course, is the classic monograph by Bramwell and Whitfield (1974) on the biomechanics of *Pteranodon*, which wedded the early functional-morphologic work of Hankin and Watson (1914) to modern concepts of aerodynamics in a beautifully written and lucid paper. According to their findings, echoed by Heptonstall (1971), Stein (1975), Sneyd *et al.* (1982), Brower (1983), and others, *Pteranodon* was a superb low-speed soaring animal that had difficulty flying in high winds and landing, but had a low sinking speed, an excellent lift/drag profile, a light wing loading, low turning radius, high manoeuvrability, and optimal performance at 7–10 m/s. It was presumed to spend most of its time gliding at sea, trapping fish at the surface in its great beak. However, its existence must have been marginal, because it was so large that

TABLE 1. Calculated aerodynamic performance of the cretaceous pterosaur *pteranodon*

| Author | W Weight (kg) | S Wing area (m ²) | Wing Loading (kg/m ²) | B Wingspan (m) | X Mean Chord (m) | AR Aspect ratio | V Speed (m/s) |
|---------------------------------|---------------------|-------------------------------------|---|----------------------|---------------------------|-----------------------|---------------------|
| von Kripp 1943* | 30 | 3.5 | 8.5 | 7 | 1 | 14 | 15 |
| | 15 | 2.25 | 6.6 | 6 | 0.75 | 16 | 13.27 |
| Heptonstall 1971 | 22.7 | 3.44 | 6.6 | 6.8 | [0.51] | 13 | 7 |
| Bramwell 1971 | 18 | 5.8 | 3.1 | 8.2 | [0.70] | 11.7 | 6.7 |
| Bramwell and Whitfield 1974† | 16.6 | 4.62 | 3.6 | 6.95 | [0.66] | 10.5 | 7.7–8.0 |
| Brower 1983‡ | 14.94 | 2.53 | 5.9 | 6.95 | [0.36] | 19.1 | 9.5 |

Values I calculated from data in other works are in brackets.

* Two configurations were given, based on different aerodynamic performance models.

† Bramwell and Whitfield (1970) considered three weight estimates (11.36, 18, and 25 kg) and used 18; in 1974 they considered 12.8, 16.6, and 23.8, accepting the intermediate value. This is very close to Brower's (1983) estimate, and reflects a range comparable to those of large modern birds.

‡ Brower calculated that *Pteranodon* could fly as fast as 17 m/s under certain conditions.

it was only barely capable of level flight; how it managed to catch fish, recover from the weight of the prey, and overcome the sudden strain on the neck to rise above the water's surface was not clear.

These studies have been very constructive in their efforts to determine parameters of flight mode, and they continue to be productive. It is worth noting, however, that most recent work on the palaeobiology of pterosaurs post-dated the aerodynamic work, and the former has important implications for the latter. Far from suggesting that aerodynamic approaches should be abandoned, I would like to provoke further discussion and investigation into the basis of understanding the aerodynamics of extinct vertebrates by raising the following questions and alternate interpretations to previous work. For some of these interpretations there is good evidence; others require only a change of attitude or modification of assumptions which are, I believe, as plausible as those of other authors.

Many palaeobiological problems, usually overlooked, relate to the structure, function, and ecology of *Pteranodon*, which was phylogenetically only a bizarre sideline of 140 million years of pterosaur evolution. Its smaller forerunners were active fliers; and *Pteranodon*, though neither the last nor the largest of pterosaurs, and not a sustained flapper, retained both limited flapping ability and full bipedal terrestrial locomotion. Any trade off of flapping ability for increased size in this lineage must have been conditional on great advantages to that way of life, and it is unlikely that millions of years of biological and aerodynamic fine-tuning would have been sacrificed in the process. Analyses of *Pteranodon's* flight have so far ignored this legacy and have overlooked or misinterpreted many important morphological factors. For example, Bramwell and Whitfield (1974) described a 'locking mechanism' in the shoulder joint of *Pteranodon* that, they argued, would have enabled the wing to be fixed in gliding position without expending much energy. This idea has been picked up by many later authors. The form of the glenoid facet, however, is not especially modified as they claim; it merely reflects the suture of the scapula and coracoid, which are fused in most adult diapsids. The corresponding 'ridge' they identify on the head of the humerus is not present on the articular surface but at its margin; this ridge is formed where the surficial laminar bone of the shaft gives way to the porous epiphyseal surface which was covered by cartilage, as was the glenoid. Therefore the 'locking joint' is very questionable. Also, the glenoid fossa faces posterolaterally, not anterolaterally as their Figure 22 shows. These factors greatly influence interpretation of the articulation and movement of the wing, which in reconstructions is almost always swept too far forward.

The structure of the wing membrane is also very important. Most aerodynamic treatments have overlooked palaeobiological considerations of the fine, stiff, intercalated 'fibres' that permeate the wing membrane (Zittel 1882; Wellnhofer 1975; Padian 1979, 1980, 1983*b*). Brower (1983) notes that they are 'approximately parallel to the wingspan [and to] the major direction of tensioning of the membrane', which is incorrect. These strong, rodlike 'fibres' of keratin or perhaps collagen are never found bent or folded, and their orientation parallels that of the feather shafts of birds and the fingers of bats (text-figs. 2, 3*c*). Hence they are precisely perpendicular to the direction of spanwise tension at any point along the wing, not parallel to it. Brower, like most other analysts, concluded that pterosaur wings, lacking internal structure, could not have been as manoeuvrable as those of bats and could not have flapped at low speeds. But it is precisely the overlooked internal structure of the wing that suggests the opposite: because the spanwise tension would have been resisted by the network of 'fibres', the wing could have been collapsed much more than in bats without loss of aerodynamic competence. Ability to draw in the wing (that is, to reduce its surface area, thereby increasing wing loading) without losing the aerodynamic competence has been denied by most authors, and so most aspects of flight performance observed in modern soaring birds have not been applied to pterosaurs. The flight of *Pteranodon* at all speeds and under all conditions has therefore been modelled as if the animal needed to keep its wings fully outstretched, which is unrealistic in view of the animal's biology.

The configuration of the pterosaur wing, as discussed earlier, was narrow and the aspect ratio high, as in a gull or albatross (Zittel 1882). Most aerodynamic analyses of the flight of *Pteranodon*

(Bramwell and Whitfield 1974; Stein 1975; McMasters 1975; Sneyd *et al.* 1982) have used a model in which the comparatively broad wings were attached to the feet, as in bats, and most of these authors have agreed that a strong tendon along the trailing edge of the wing, anchored to the feet, would have been necessary to control the membrane (text-fig. 3C, *left*). In fact, preserved wings of pterosaurs show incontrovertibly both that the hindlimbs were free of the wing and that no trailing wing tendon existed: further evidence for the structural integrity of the 'fibres'. Without these fibres, a strong trailing tendon would have been necessary, and in that case it would indeed, as aerodynamicists have argued, been very difficult for *Pteranodon* to draw in the wing at all without collapsing it. Furthermore, the extreme forward sweep of the wings commonly pictured (e.g. Bramwell and Whitfield 1974; Brower 1983; Sneyd *et al.* 1982) was impossible, being based on incorrect anatomical interpretations and the assumption of a wide wing. With a narrow wing and correct articulations, the centre of lift is further back, and the wing profile slimmer and more laterally directed (text-fig. 3C, *right*).

What are the aerodynamic consequences of these considerations? Only Brower (1983) has used a narrow wing configuration in aerodynamic calculations, and his calculated wing area is 55% of that used by Bramwell and Whitfield and others. (My own estimate is closer to 45%.) The wing loading is then effectively doubled, which has a significant effect on calculated flying and sinking speeds, polar curves, turning radius, mass distribution, and flapping performance. These will be considered in detail elsewhere, but it may be noted for instance that the wing chord and induced drag are halved, and wing profile drag is probably no longer comparable to that of the Gottingen 417a airplane, which lacks the large leading spar of the pterosaur's wing and is very dissimilar to it in aspect and cross-section.

Accepting that the wing did not lose its shape (i.e. its aerodynamic competence) when partially drawn in, *Pteranodon* need no longer be considered only in fully extended position. The larger wing loadings, higher flying speeds, and lower sinking speeds that result are characteristic of the performances of modern soaring birds. For instance, Bramwell (1971) calculated that in a typical thermal *Pteranodon* would gain half a mile in altitude in five minutes. But what if *Pteranodon* wished to use the thermal to search for food without gaining altitude? One can now see that it had only to flex the wings to achieve lower wing area, higher wing loading, greater airspeed, and even lower sinking speed. Using Bramwell's configurations and calculations, a thermal rising at 4.1 m/s would have carried *Pteranodon* up at a rate of about 3.45 m/s. This value is also her calculated sinking speed at a flying speed of 16.5 m/s. Therefore *Pteranodon* could have flown level in a thermal at 16.5 m/s. This is more than twice the calculated 'optimal' flying speed in still air, and the wings are fully outstretched. How would *Pteranodon*'s performance improve if the ability to flex the wings to control flight were considered?

In general, a palaeobiological view of *Pteranodon*'s flight appears to give greater ranges for most calculated flight variables: higher speeds, more manoeuvrability, and better take off and landing performance. The typical calculated polar curve of *Pteranodon* (e.g. Bramwell and Whitfield 1974; Brower 1983) is much more attenuated compared to those of birds and aircraft; but of course, the latter curves were discerned by empirical observation, not by calculation. What would happen if values for albatrosses and falcons were calculated based on the kinds of data estimates used for *Pteranodon*, and then compared with empirical results? Until this is done there is no way to judge the accuracy of approaches that have so far been taken to pterosaur flight. Pterosaurs were not aircraft, and their wings were in no way comparable to those of hang-gliders (*contra* Brower 1983 and McMasters 1975) or sailplanes (*contra* Bramwell and Whitfield 1974); nor were their wing skeletons inflexible spars with the membranes under considerable spanwise tension (*contra* these authors and Sneyd *et al.* 1982). Their wings were comparable in biological and aerodynamic respects to the wings of birds and bats, with a design inherited from their ancestors, shaped by natural selection, and fine-tuned by evolutionary constraints and opportunities. Until these factors are considered in engineering approaches, we shall probably lack a realistic view of the flight performance of pterosaurs, and continue to view them as inferior precursors to birds and bats.

CONCLUSION

Over the past two decades knowledge of animal flight has deepened considerably. Much more is known of the mechanics of flight, and the ability to calculate flight energetics accurately (see Pennycuik 1972) augurs well for the understanding of the evolution of flight and for the significance of the differences among modern flyers in the physiology of flight. Preliminary results of the attempts to fuse engineering with palaeontology to arrive at realistic appraisals of the flight performances of extinct taxa have been pioneering in their approaches. Yet most of this work has yet to take advantage of recent palaeobiological advances in the phylogenetic and functional understanding of these animals. If, as current research indicates, birds evolved from small theropod dinosaurs and developed flight from the ground up, the utility of studying gliding performance in *Archaeopteryx* is uncertain; the earliest birds may seldom, if ever, have glided. The main problem is still getting up in the air and staying up, which requires a realistic analysis of the evolution of flapping. In pterosaurs the efficiency of the wings as flying organs seems to have been underestimated, because considerations of the aerodynamics and functional morphology of the large soaring form *Pteranodon* have neglected the functional and phylogenetic evolution of pterosaurs. Bats, unfortunately, remain largely shrouded in mystery with respect to the means by which they evolved flight; it can be hoped that as their phylogenetic relationship with other mammals is clarified, the characteristics clearly distinguishing bats from these groups may shed light on the evolution of flight in these most unusual of flying vertebrates.

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